Experiments on downstream movement of recently emerged trout and salmon parr in Grassholme channels, 1983-1985.

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CONTENTS

SUMMARY

1. The report describes the results of investigations on the timing and rate of downstream movement of young brown trout (Salmo trutta L.) and Atlantic salmon (Salmo salar L.) out of experimental channels, with special reference to the effect of water velocity on the rate of "emigration".

2. The effect of water velocity on emigration was examined by the application of four different nominal mean velocities (7.5, 25.0, 40.0 & 70.0 cm s^{-1}) in a Latin square design and three experiments were performed on each of the two fish species.

3. Trout showed a low rate of emigration at 25 cm s^{-1} velocity, a higher value at 7.5 cm s^{-1} and increasing values at 40 and 70 cm s^{-1}. This pattern was common to all three experiments and the differences between the effects of the treatments were significant in two of the three experiments.

4. Salmon showed a high emigration rate at 7.5 cm s^{-1} and much lower rates at 25 to 70 cm s^{-1}. This pattern was common to all three experiments and the differences between the effects of the treatments were significant in two of the three experiments.

5. No effect of population density upon emigration rate could be detected for salmon, but a significant effect was shown for trout.

6. Experiments at constant channel velocities showed that, for both species, emigration rate was negligible before swim-up, increased rapidly after swim-up and then decreased again. The trout experiment suggested that, although emigration rate might vary with velocity treatment, the

final population density would be similar under all velocity treatments. Hence, the rate at which the final density was attained (and the duration of relatively high rates of emigration) would depend upon the rate of emigration. The results of the salmon experiment led to similar conclusions except that at the lowest velocity (8 cm s^{-1}) there was a very high rate of emigration and the population density at the end of the experiment was very low (1.8 fish m^{-2} c.f. 5-8 fish m^{-2} at higher velocities).

7. At constant water velocities c. 97% of both trout and salmon leaving the channels did so by night rather than by day ($P<0.001$).

INTRODUCTION

A number of authors have described the manner in which young salmonids, soon after emergence from the gravel, set up and defend territories. This leads to mortality or downstream displacement of the individuals which are unable to acquire territories and is widely accepted as the main method of population regulation amongst young salmonids. In some field experiments (e.g. Le Cren, 1973) the fish were constrained in screened reaches and the option of downstream dispersal for the surplus fry was thus excluded. Other observers (e.g.s Egglishaw & Shackley, 1977; Elliott, 1984) did not measure downstream dispersal in any detail but assumed either that such dispersal was negligible or that the fish so dispersed were moribund and therefore dispersal was equivalent to mortality.

The published evidence suggests that these losses (by mortality and/or dispersal) are density-dependent but Kalleberg (1958) noted that territory size was influenced by water velocity. It is, therefore, possible that the coefficients of the density relationship will be modified by water velocity.

In order to explore some aspects of downstream dispersal more closely under conditions which gave more control than is obtained in a natural stream, four experimental channels were set up at Grassholme reservoir in Teesdale (NY 947229). A brief description of the channels and the results of preliminary experiments in 1980 and 1981 were given by Ottaway & Clarke (1981)and Ottaway & Forrest (1983). However, these experiments were open to criticism in terms of experimental design and data treatment and further experiments were performed in 1983, 1984 and 1985.

In the 1983 experiments, salmon and trout were subject to water velocity regimes which changed daily over a four day period and the number of fish leaving the lower end of each channel each day was recorded. These experiments gave information on the relationships between water velocity, population density and rate of downstream dispersal and provided four replicates of each treatment. In the experiments of 1984 (trout) and 1985 (salmon) each channel was stocked with fish which had not completely absorbed their yolk sacs. They were allowed to bury themselves in the gravel and then each of the four channels was run at a different constant velocity and numbers of fish leaving the channels were recorded daily. These experiments provided information on temporal variation in rate of downstream dispersal, but without replication of the treatments. During the 1984 and 1985 experiments additional observations were made on the partitioning of downstream movement between daytime and night.

METHODS

The apparatus consisted of four fibreglass channels each with a working length of 10.7 m a width of 0.99 m and a depth of 0.45 m (working area 10.6 m^2). The channels were filled to a depth of 12.5 cm with a mix of washed Dogger Bank gravel (Table 1). Discharge in each channel was controlled by a valve at its upstream end and the balance between velocity and depth was controlled by a tailgate at the downstream end. Fish leaving the downstream end of each channel were collected in a large nylon meshed net whose lower end was immersed in the river.

TABLE 1. Composition of the gravel used in the channels from Carling (1984). Statistics of the frequency distribution are: Arithmetic mean = 15.57 mm, Standard deviation = 8.10 mm, Skewness = 0.54, Kurtosis = 2.22. Note that the ϕ scale is an expression of particle sizes on a $\log_2$ basis and $\phi = 0$ when particle size = 1 mm.

Particle size range (mm)	ϕ	% composition
32 - 16	- 4.5	41.71
16 - 8	- 3.5	34.73
8 - 4	- 2.5	22.84
4 - 2	- 1.5	0.69
2 - 1	- 0.5	0.01
1 - 0.5	+ 0.5	0.03

Use of finer and more uniform gravel than that employed in the pre-1982 experiments gave greater uniformity of flow within the channels and permitted more accurate calibration. Extensive calibration work during 1982 showed that, despite this, under any given channel setting, there was significant ($P<0.05$) spatial variation in water velocity at 0.6 of depth within each channel. On a transect 5.5 m downstream of the top of each channel the experimental treatments were responsible for 86% of the total sum of squares for depth and 92% of the total for velocity, whereas spatial variation across the width of the channels, repetitions of treatment, variation between channels and two-way interactions each accounted for less than 2% of the total sum of squares for depth or velocity. It should be noted, however, that, within any given treatment, there was appreciable variation in depth and velocity along the length of each channel (Crisp & Hurley, 1984).

Four standard regimes were applied during the experiments (Table 2A).

During the course of each experiment the nets at the downstream ends of the channels were emptied daily and the fish caught were measured and weighed. At the close of each experiment the residual fish were removed and enumerated by electrofishing. A technique was devised which usually gave efficiencies of capture on single fishings of 50-90% so that six successive fishings could be expected to account for over 98% of the residual population. The 95% C.L. on estimates of residual population based on the first four fishings only were generally $< \pm 2\%$ for trout (mean = $\pm 1.1\%$) and <15% for salmon (mean = $\pm 4.2\%$) (Crisp, 1983).

The 1983 experiments were a redesigned version of those described by Ottaway & Clarke (1981). Between 18 April and 25 June 1983 six experiments, designated E_1 .....E_6, were performed on trout (T) (Salmo trutta L.) and salmon (S) (Salmo salar L.) fry at various stages of development. In experiments E_1T, E_2S, E_3T and E_6S each channel was stocked with 212 fish (20.0 m^{-2}). In experiments E_4S and E_5T smaller numbers of fish were used (Table 4). The fish were

TABLE 2. General design of the 1983 channel experiments. (A) Details of the four treatments, denoted by the letters a-d. Each treatment is a combination of a nominal velocity and a nominal depth.
(B) The five "regimes", or combinations of treatments, used in the 1983 experiments. Note that regime 1 (lowest velocity in all four channels) was used at the start and finish of each experimental run.

A.

Treatment	Nominal mean velocity(cm s^{-1})	Nominal mean depth(cm)
a	7.5	5.4
b	25.0	9.8
c	40.0	12.3
d	70.0	16.2

B.

Regime	Duration of regime(h)	Channel	1	2	3	4
			Treatments			
1	3		a	a	a	a
2	24		a	d	c	b
3	24		b	c	d	a
4	24		c	b	a	d
5	24		d	a	b	c
1	72		a	a	a	a

released into the channels at 0600 hours on the first day, with all four channels set at a low velocity (Regime 1) (Table 2B). At 0900 hours the channel nets were emptied and the channels were set to regime 2 (Table 2B). Thereafter, the nets were emptied daily at 0900 hours and the experimental regimes were changed at the same time in a Latin square pattern. Finally, all four channels were set at low velocities for three days and the residual fish were removed by electrofishing.

The experiments of 1984 on trout and 1985 on salmon followed the general pattern outlined by Ottaway & Forrest (1983). They stocked the channels with fertilized eggs and then ran the four channels at four different constant velocities and counted the fish emerging from the lower end of each channel. Interpretation of the results presented difficulties because no precise estimate of egg mortality was obtained and the population density of fry at the time of emergence from the gravel could not be estimated accurately. In the 1984 and 1985 experiments each channel was stocked with 1,000 trout alevins (94.4 m^{-2}) and 600 salmon alevins (56.6 m^{-2}) respectively, shortly before "swim-up" was expected, with all four channels under treatment "a" (Table 2A). The fish were allowed one hour to bury themselves in the gravel. The channels were then set at four different treatments (Table 3) and fish leaving the channels were counted daily.

TABLE 3. Mean water depth and velocity in each channel during the 1984 & 1985 experimental treatments.

Channel	Mean water depth (cm)	Mean water velocity (cm s^{-1})
1	14.5	69.3
2	8.5	8.0
3	12.7	27.1
4	15.9	49.9

MATERIAL & GENERAL TREATMENT OF RESULTS

The dates and water temperatures of the experiments are shown in Table 4, together with initial stocking densities and mean weights and lengths of the fish material. Problems arise in defining stage of development. This cannot be adequately done in terms of the age, length, or weight of the fish. Therefore, to provide a criterion which has at least some physiological validity, development has been defined in terms of percentage development to median hatch date predicted from recorded water temperatures and the equations of Crisp (1981). In general, 50% swim-up (emergence from the gravel) occurs somewhere between 150 and 200% of development to median hatch (i.e. at a constant temperature, swim-up occurs after 1.5 to 2.0 times the number of days required for median hatch).

During each experiment there was a discrepancy between the number of fish initially stocked and the numbers accounted for in net catches and in the final electrofishing. This has been assumed to represent mortality within the channels occurring at a constant instantaneous rate throughout the experiment. In the 1983 experiments the estimated percentage of input fish lost through mortality varied between experiments but averaged 14% for trout and 18% for salmon over a period of 171 hours. In the 1984 trout experiment mortality averaged 16.5% over a period of 64 days. In the 1985 salmon experiment mortality averaged 16% over 28 days.

The data on rate at which fish left the lower end of each channel were expressed as instantaneous daily rates of "emigration", though the use of this term should not be assumed to carry any implication about whether the departure from the channels was voluntary or otherwise. For each channel, during each experiment, an estimate of daily rate of instantaneous mortality was made by a process of iteration until a value was found which

TABLE 4. Details of experimental temperatures and material. The trout were all descendants of hatchery stock. The 1983 salmon were reared from Scottish ova and the 1985 salmon were from R. Tyne ova.

Note: i. The salmon used in E_2S were barely at the swim-up stage.

ii. The trout used in E_3T were an equal mixture of two different developmental stages.

iii. The low stocking density in E_5T was a result of shortage of material.

Experiment	Dates	Temp. range (°C)	Initial no. m^{-2}	Initial mean length (cm) ± 95% C.L.	Initial mean weight (g) ± 95% C.L.	Predicted % development to median hatch at start of experiment
1983						
E_1T	18-22 April	4.7 - 4.8	20	2.6 ± 0.06	0.15 ± 0.0075	194
E_2S	26-30 April	5.1 - 5.4	20	2.4 ± 0.06	0.13 ± 0.0107	173
E_3T	9-13 May	6.4 - 6.6	20	2.6 ± 0.08	0.13 ± 0.022	178 - 233
E_4S	17-21 May	7.1 - 7.2	19	2.6 ± 0.04	0.12 ± 0.006	200
E_5T	13-17 June	10.2 - 11.2	6	2.7 ± 0.03	0.16 ± 0.007	219
E_6S	21-25 June	11.2 - 11.8	20	2.7 ± 0.05	0.15 ± 0.009	224
1984						
T	16 April-19 June	5.5 - 11.4	94	2.2 ± 0.05	0.14 ± 0.006	153
1985						
S	24 May-20 June	9.3 - 10.9	57	2.6 ± 0.03	0.13 ± 0.004	150

was consistent with the numbers present at the start of the experiment, the numbers present in the channel at the end of the experiment and the numbers of fish known to have emigrated each day. This rate of mortality was then used in calculating the number of fish present at the start and end of each day and the mean population density during that day. It was then possible to express the number of fish emigrating from each channel each day as an instantaneous rate, relative to the number present at the start of that day.

These general approaches were used in processing the results of all the channel experiments. The details of data processing were specific to each series of experiments and are covered at appropriate points in the presentation of results.

RESULTS

1. Experiments on the effects of changing water velocity upon downstream movement of recently-emerged salmon and trout (1983).

Within these experiments fish were lost from the channels by emigration and death. For simplicity, a constant instantaneous rate of mortality has been assumed in each channel during each experiment (Table 5) and the rate of emigration has been assumed to be influenced by experimental treatment (water velocity), the individual channels, and the elapsing of time and/or changes in the population density of the fish during the course of the experiment. The various interrelationships have been analysed by

TABLE 5. Estimated mean instantaneous mortality rates (M) day^{-1} during the experiments. $M = \ln N_0 - \ln N_1$ where N_0 is number of fish present at the start of the day and N_1 is the number present at the end of of the day and there is no loss by emigration.

Channel	1	2	3	4
Experiment	Estimated mean instantaneous mortality rate day^{-1}			
1983				
E_1T	0.050	0.065	0.076	0.059
E_3T	0.033	0.031	0.052	0.031
E_5T	0.087	0.036	0.021	0.017
E_2S	0.090	0.074	0.090	0.095
E_4S	0.021	0.026	0.023	0.022
E_6S	0.065	0.045	0.074	0.035
1984				
T	0.0040	0.0023	0.0029	0.005
1985				
S	0.0085	0.0034	0.0055	0.0074

means of the "Glim" computer package (Hurley, in prep.) with a binomial error, a complementary log-log link and using the number emigrating as the y variable and the estimated number available to emigrate as the binomial denominator. Details of the statistical approach are given by Hurley (in prep.) with regard to the simplified method outlined above and a rigorous method. The former has been followed here, because the two approaches give very similar results for the experiments described.

Daily instantaneous rates of emigration from the channels were examined relative to the effects of differences between channels, experimental treatment (water velocity), time (day number during the experimental sequence) and fish population density. The analyses for time and population density presented complications because population density reduced with time through each experiment. The effects of these two factors were tested by first adding time followed by density and then adding density followed by time to the model containing channel and treatment effects. When the addition of density alone had a significant effect this demonstrated that emigration rate was, in part, density-dependent. When the addition of time after density had a significant effect this indicated that circumstances other than density had changed with time and had influenced emigration. From the analysis of density and time a reference model was selected with which to test the additional effect of treatment. The model chosen contained the effects of channel and time unless the effect of time was solely a result of population density change, in which eventuality the reference model contained the effects of channel and density. The effect of the channel was assessed by testing the reduction in explanation when the channel effect was excluded from the final model (i.e. the reference model with treatment included).

TABLE 6. Table to show the significance in each experiment of the effects studied. N.S. = $P>0.05$, * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$.

Experiment	Channel	Time	Population density	Treatment
E_1T	N.S.	**	**	N.S.
E_3T	N.S.	N.S.	**	***
E_5T	N.S.	*	*	*
E_2S	N.S.	N.S.	N.S.	**
E_4S	N.S.	N.S.	N.S.	**
E_6S	N.S.	N.S.	N.S.	N.S.

TABLE 7. Summary of appropriate models and of constants to substitute in the models in order to predict emigration rate in each experiment, channel, treatment and day.

Expt.	Model	Constant	Channel				Day				Popn.	Treatment			
		(K)	C_1	C_2	C_3	C_4	t_1	t_2	t_3	t_4	density(β)	U_a	U_b	U_c	U_d
E_1T	$\ln Rate = K+C_i+\beta d+U_k$	-4.87	0	0.62	-0.77	-0.84	-	-	-	-	0.028	0	-0.97	-0.71	-0.21
E_3T	$\ln Rate = K+C_i+\beta d+U_k$	-3.72	0	0.49	-0.34	-0.10	-	-	-	-	0.011	0	-1.08	0.13	1.14
E_5T	$\ln Rate = K+C_i+t_j+U_k$	-1.42	0	0.20	0.10	-0.11	0	-0.48	-0.25	-3.42	-	0	-0.74	0.50	1.18
E_2S	$\ln Rate = K+C_i+t_j+U_k$	-2.62	0	0.53	-0.19	0.31	0	-1.98	0.14	-0.70	-	0	-2.58	-2.91	-2.57
E_4S	$\ln Rate = K+C_i+t_j+U_k$	-1.69	0	0.25	0.54	0.83	0	-1.22	-0.63	-0.55	-	0	-2.50	-2.42	-1.88
E_6S	$\ln Rate = K+C_i+t_j+U_k$	-1.69	0	0.10	0.21	-0.52	0	0.12	0.22	0.23	-	0	-1.01	-0.91	-0.52

The results (Table 6) did not demonstrate any significant effect of the channels in any experiment nor of time or population density in any of the salmon experiments. In the trout experiments there was a significant effect of population density in all three experiments but in E_5T the analysis indicated that circumstances other than fish density also changed with time during the course of the experiment. The experimental (water velocity) treatments had a significant effect in two out of three trout experiments and in two out of three salmon experiments.

Details of the final models for estimating ln (daily instantaneous rate of emigration) in each channel, on each day of the experiment and under each experimental treatment are given in Table 7, together with values of the appropriate parameters.

Plots of relative emigration rate (where rate is relative to a value of 1.0 at the lowest velocity treatment) when the effects of other factors are held constant, are shown in Fig. 1. The plots show clear differences between the species. Emigration rate for trout showed a minimum under treatment "b" (25 cm s^{-1}) and increased at higher water velocities. In contrast, salmon showed a high rate under treatment "a" (7.5 cm s^{-1}) and much lower rates at higher water velocities. These patterns were common to all three experiments within each species, though the intensity of the water velocity effect varied between experiments within each species and this is reflected by the significance levels (Table 6). For salmon parr in E_2S and E_4S water velocities of 25-70 cm s^{-1} reduced emigration rate to 50% or less of the value observed at 7.5 cm s^{-1}. For trout parr in E_3T and E_5T the rate of emigration at 70 cm s^{-1} was at least 150% of the value at 7.5 cm s^{-1}.

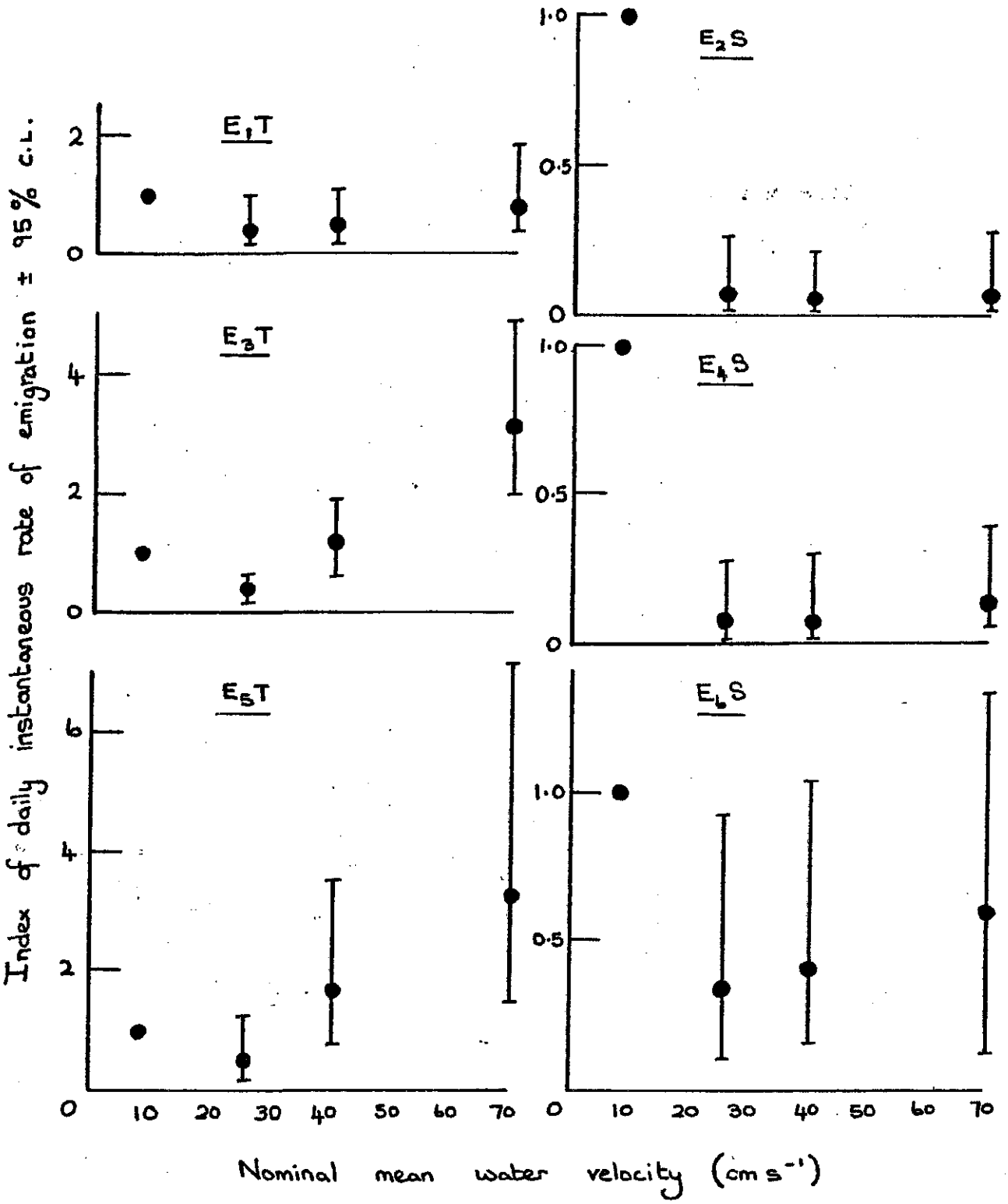

Figure 1. Plots of mean daily instantaneous rates of emigration (adjusted to give a value of 1·0 under treatment "a" (7·5 cm s^{-1}) ± 95% C.L. against nominal mean channel water velocity at 0·6 of depth. Note differences in rate scales between different experiments.

2. Experiments with trout using four constant water velocity treatments during the weeks preceding and following emergence from the gravel (1984).

Daily mean temperatures during the experiment are shown in Figure 2a. Trout material was introduced into the channels on 16 April, 1984 and details are given in Table 4. The predicted date for 50% hatch was 7 February and the observed date was 12 February (at predicted 103% development to median hatch). The estimated rates of natural mortality during this experiment were an order of magnitude lower than those in the 1983 experiments (Table 5). Estimated emigration rates in all four channels (Figure 3) were very low until the end of the first week in May and they then increased, though the temporal pattern of fluctuation in emigration rate varied between channels. The end of the first week in May coincided with the absorption of the yolk sac (Figure 4) and emergence from the gravel and occurred at a time when predicted development to median hatch was c. 180%.

In all four channels, rate of emigration increased rapidly with time from the end of the first week of May onwards. In the channel with the lowest velocity treatment (8.0 cm s^{-1}) rates fluctuated between 0.01 and 0.10 day^{-1} throughout the remainder of May and most of June. In the other three channels the rate rose rapidly to peak values of 0.08 to 0.24 day^{-1} in mid-May and then reduced rapidly to values of 0.03 or less by the end of May. These results suggest that high rates of emigration occur soon after emergence from the gravel and then reduce rapidly. It is not clear whether the reduction simply represents the passage of time, per se, or whether it reflects reduction of population density and continues at a high rate until population density has been reduced to a suitable level.

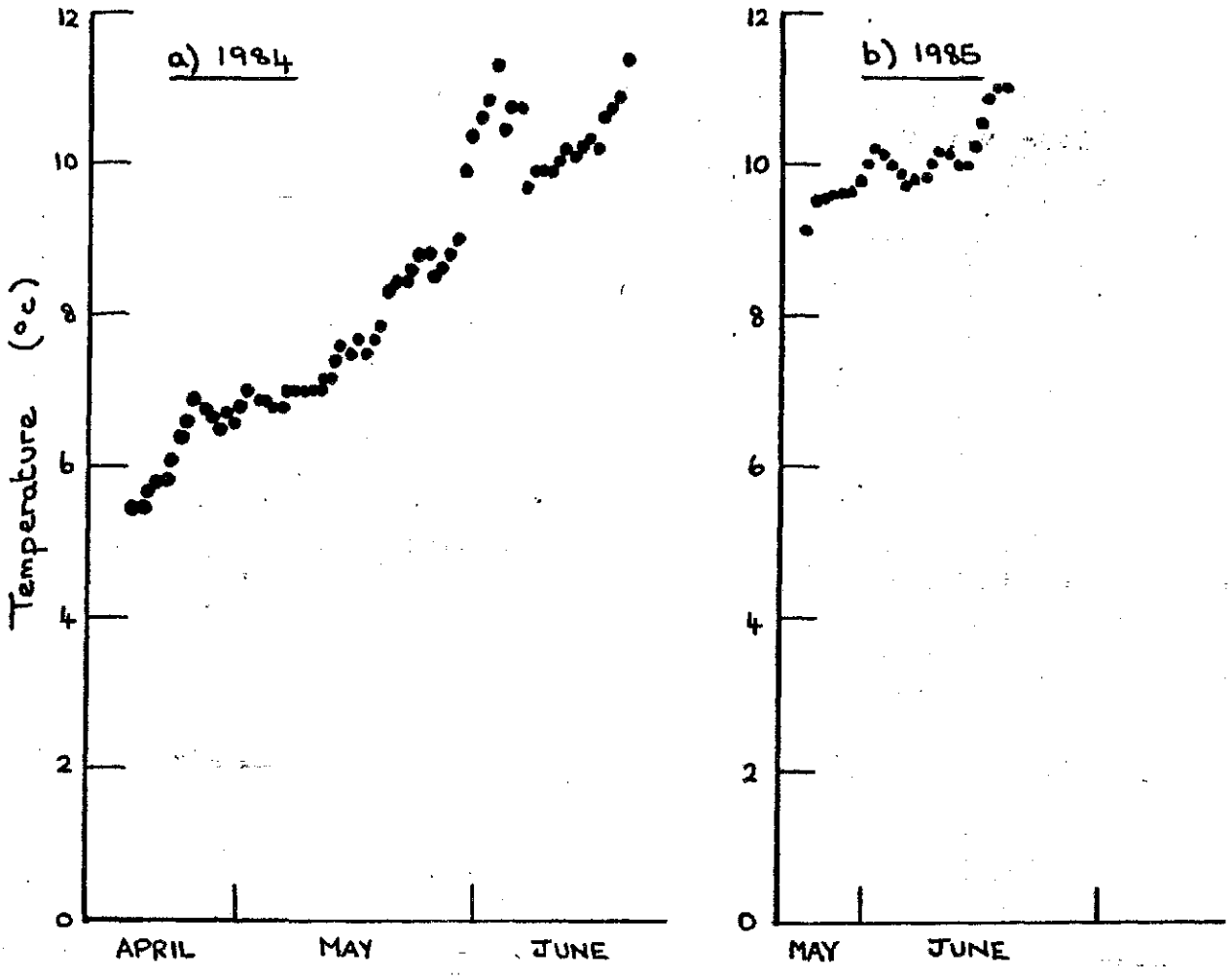

Fig. 2. Daily mean water temperatures during 1984 and 1985 channel experiments.

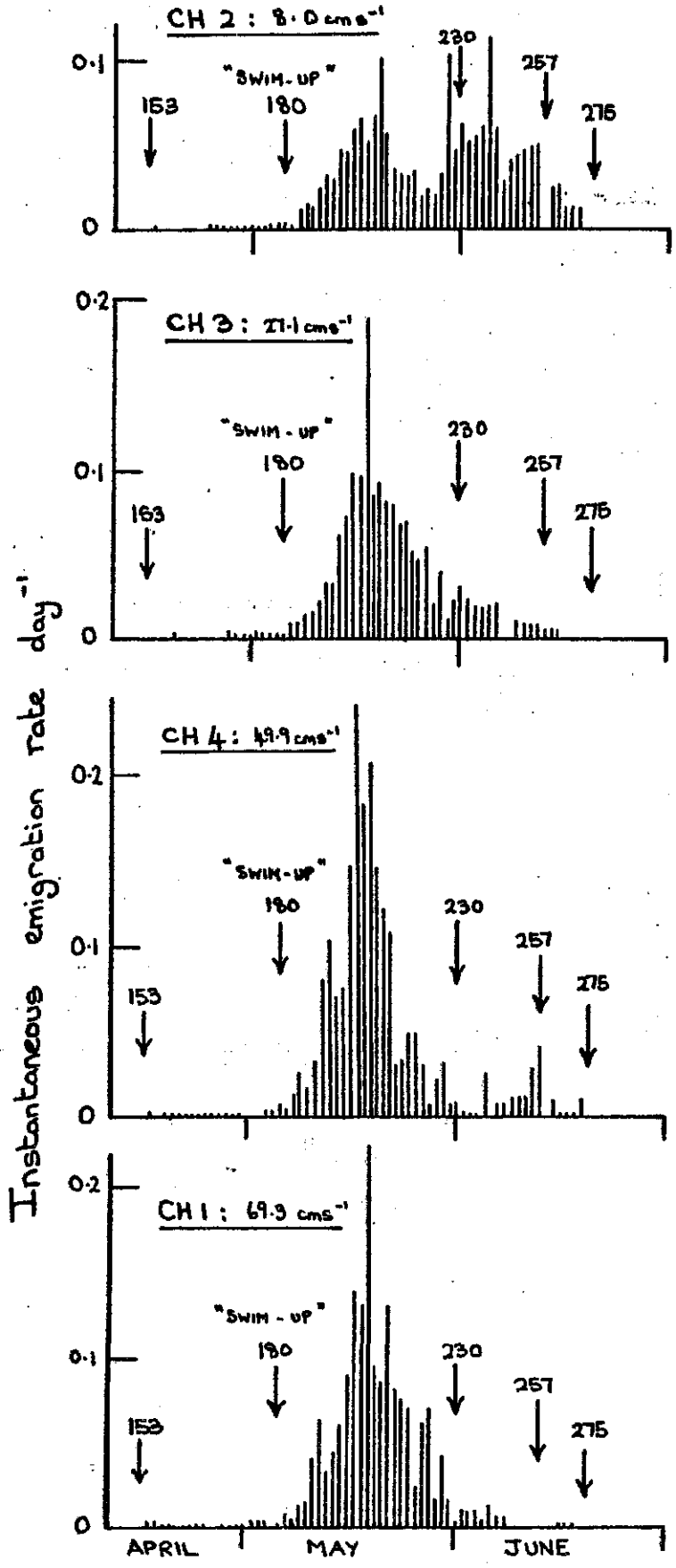

Fig. 3. Plots of instantaneous emigration rate day^{-1} against time during the 1984 channel experiment. % completed development to median hatch is shown for the start and end of the experiment, for the time of emergence from the gravel and for the 1st and 12th June.

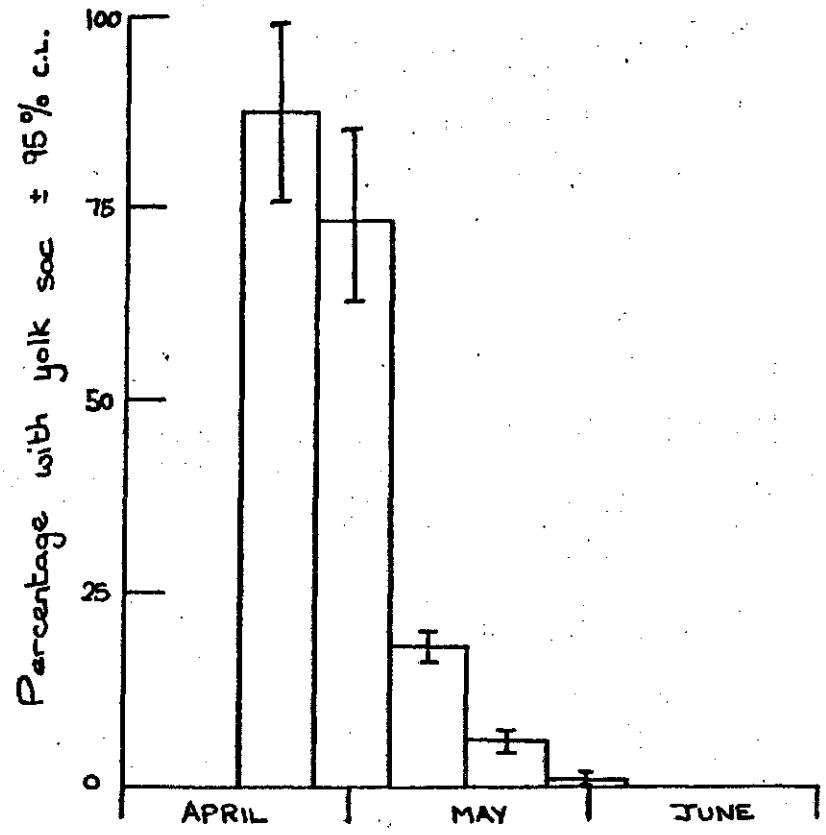

Fig. 4. Percentage (± 95 % c.l) of fish with some yolk sac still visible, amongst fish caught in the channel nets during each 10 day period of the 1984 experiment.

However, the extended period of emigration at a low rate in the channel at the lowest velocity (8.0 cm s^{-1}) suggests the latter, as also does the fact that a similar population density was attained in all four channels by the end of the experiment (Table 8).

A summary of estimated population density at the end of the experiment and of growth and production during the experiment is shown in Table 8. None of these showed any clear-cut pattern relative to velocity treatment though treatment "b" was associated with the highest values of density, growth and production. Instantaneous growth rate (y) could be related to initial mean fish weight (x) in each channel by the equation $y = 0.042 x - 0.0001$ ($r = 0.9998$, $P<0.01$). The proportions of total production lost by mortality and emigration and remaining alive in the channels at the end of the experiment were c. 10, 64, and 27% respectively. There was no clear-cut pattern of apportionment between the three categories which reflected water velocity treatment.

During the period of peak emigration rates in mid-May the channel nets were examined twice within each of three periods of twenty-four hours. The results (Table 9) showed that about 96% of fish leaving the channels did so during the portion of the day which contained the hours of darkness and that the difference between numbers leaving by nibht and by day was statistically significant ($P<0.001$).

TABLE 8. Summary of growth, survival and production during the 64 days of the 1984 experiment and the 28 days of the 1985 experiment. At the starts of the experiments there were 94 trout m^{-2} (1984) and 57 salmon m^{-2} (1985).

Channel No.	Mean water velocity (cm s^{-1})	Est. popn. density at end of expt. (No. m^{-2}) ± 95% C.L.	Mean weight per individual at end of expt. ± 95% C.L.	Mean production g m^{-2} day^{-1}	Inst. growth rate day^{-1}	% of production		
						Died	Emigrated	Remained
1984 trout								
2	8.0	13.9 ± 0.27	0.3555 ± 0.0201	0.0887	0.0148	7.74	65.77	26.49
3	27.1	16.6 ± 2.16	0.3988 ± 0.0171	0.0925	0.0166	8.36	56.67	34.97
4	49.9	8.6 ± 0.29	0.3632 ± 0.0207	0.0731	0.0151	13.09	68.71	18.20
1	69.3	12.4 ± 2.06	0.3815 ± 0.0152	0.0815	0.0159	10.83	63.12	26.05
1985 salmon								
2	8.0	1.8 ± 0.25	0.1672 ± 0.0137	0.0317	0.0087	2.92	93.34	3.74
3	27.1	7.9 ± 0.50	0.1676 ± 0.0062	0.0255	0.0087	6.43	77.74	15.83
4	49.9	4.9 ± 0.18	0.1603 ± 0.0073	0.0271	0.0072	7.67	82.44	9.89
1	69.3	7.3 ± 0.66	0.1621 ± 0.0072	0.0229	0.0079	8.61	76.63	14.76

TABLE 9. Numbers of trout emigrating from the channels by "day" and by "night" on each of three days during 1984. Each day was a period of approximately 24 hours (c. 0900 hrs to c. 0900 hrs) and was separated into two approximately equal periods of day (c. 0900 hrs. to c. 2100 hrs and c. 2100 hrs to c. 0900 hrs) so that the "night" period included the hours of darkness. The expected ratios of catches were based on the number of hours during the "day" and "night" periods.

Dates		Day	Night	Expected ratio (day:night)	Chi-squared	P
11 - 12 May	Observed	6	157	0.44 : 0.56	107.5	<0.001
	Expected	71.7	91.3			
12 - 13 May	Observed	4	160	0.42 : 0.58	105.3	<0.001
	Expected	68.9	95.1			
13 - 14 May	Observed	6	161	0.44 : 0.56	110.7	<0.001
	Expected	73.65	93.5			

3. Experiments with salmon, using four constant water velocity treatments preceding and following emergence from the gravel (1985).

Predicted development to median hatch was 150% at the time of introduction to the channels. However, inspection of the material showed quite clearly that the there was a bimodal distribution of developmental stages. Most of the alevins had appreciable residual yolk but a substantial minority had negligible yolk reserves and appeared to be on the point of swim-up. These latter fish left the channels at high instantaneous rates (0.2 to 0.45 day^{-1}) during the two days following introduction (Figure 5). After this, emigration rates were low (<0.05 day^{-1}) until 4 June at 170% of estimated development to median hatch, when the majority of the salmon emerged from the gravel and emigration rates at the three highest velocities rose to values of 0.1 to 0.25 day^{-1} and then decreased. At the lowest velocity higher rates of emigration (up to 0.35 day) occurred and were maintained almost to the end of the experimental period.

Instantaneous growth rate during the course of the experiment (y) (Table 8) showed no obvious relationship to velocity treatment but could be related to initial mean weight per fish in each channel by the equation $y = 0.19x - 0.024$ ($r = 0.9783$, $P<0.05$). Final population density at the lowest velocity value was very low (1.8 m^{-2}). The other three channels had higher final population densities (4.9 - 7.9 m^{-2}). Neither mean instantaneous growth rate nor mean production showed any clear pattern which could be related to channel velocity, though the percentage of total production which emigrated was higher at the lowest velocity than in the other three channels. Instantaneous growth rate and estimated production were lower for salmon than for trout, whilst the percentage of production which emigrated was higher for salmon than for trout. These differences are probably largely attributable to differences in the duration of the two experiments. As for trout, 96-98% of the fish leaving the channels did so by night (Table 10) and the difference was statistically significant ($P<0.001$).

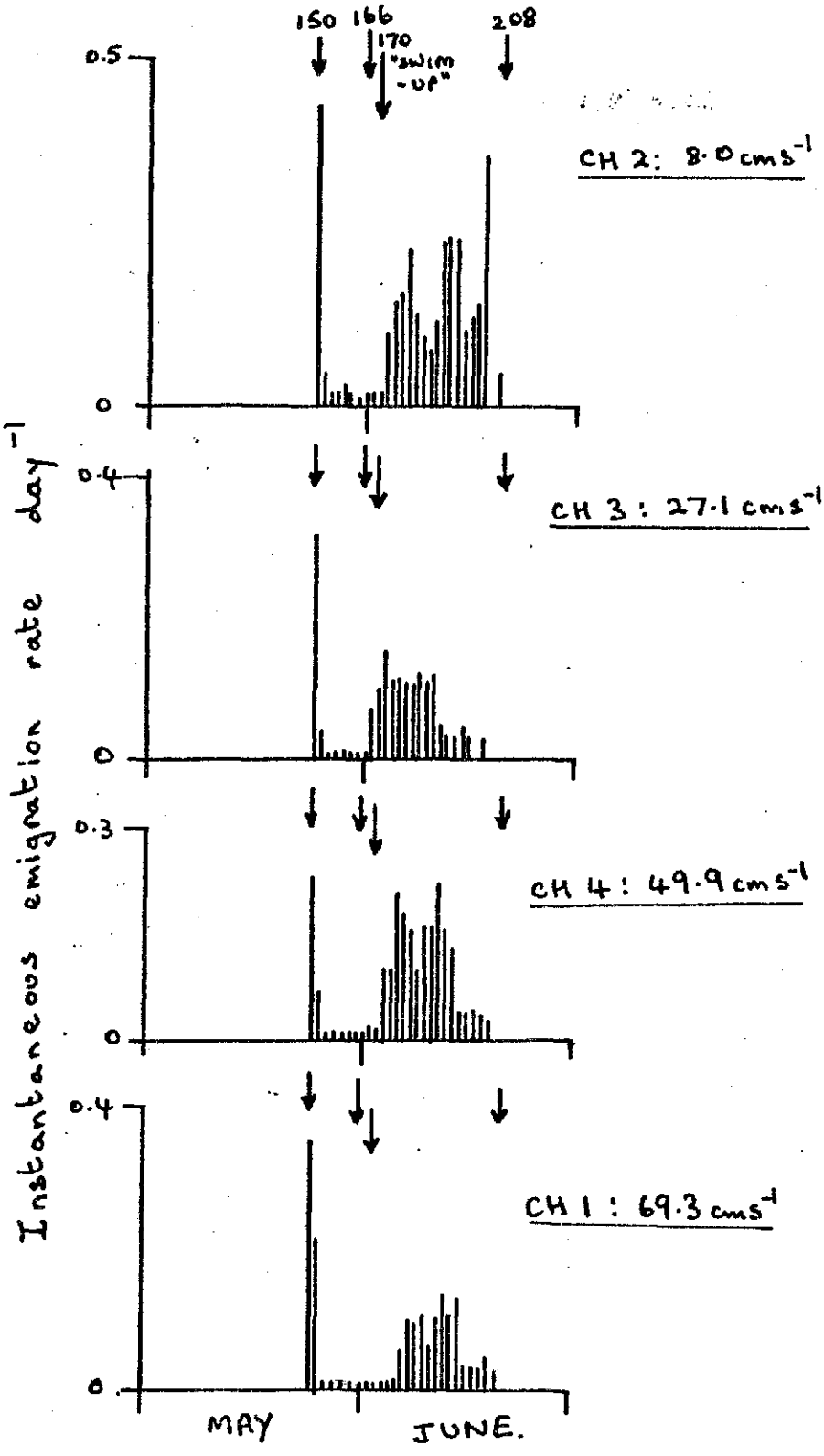

Fig. 5. Plots of instantaneous emigration rate day^{-1} against time during the 1985 channel experiment. % completed development to median hatch is shown for the start and end of the experiment, for the time of emergence from the gravel and for 1ST June.

TABLE 10. Numbers of salmon emigrating from the channels by "day" and by "night" on each of two days during 1985. Other information as in Table 9.

Dates		Day	Night	Expected ratio (day:night)	Chi-squared	P
5-6 June	Observed	5	142	0.51:0.49	133.4	<0.001
	Expected	75	72			
6-7 June	Observed	3	123	0.52:0.48	124.2	<0.001
	Expected	65.5	60.5			

CONCLUSIONS & DISCUSSION

It is important to note that the 1983 experiments were specifically designed to test the effects of different velocity treatments upon the rate of downstream dispersal, whereas the main aim of the 1984 and 1985 experiments was to identify the stage(s) of development at which those effects operated with the greatest intensity. In 1984 and 1985 the velocity treatments were not replicated and each channel had a different constant velocity over a relatively long period of time. In consequence, during the course of the 1984 and 1985 experiments, differences between channels which were additional to differences inherent in the channels themselves or in the velocity treatments became apparent. Particularly noticeable was differential growth of filamentous algae, though this was also likely to have been accompanied by quantitative and/or qualitative differences in benthos.

The 1983 experiments showed that water velocity had a significant effect on the rate of emigration of young salmon and trout, though the relationship differed between the two species, the intensity of the effect varied between experiments within a species and an additional effect of population density was apparent for trout but not for salmon. Salmon had high rates at the lowest velocity (8 cm s^{-1}) and much lower rates at the three higher velocities, whereas trout had a low rate at c. 27 cm s^{-1}, a rather higher rate at 8 cm s^{-1} and even higher rates at 50 and 69 cm s^{-1}. These effects were only very approximately reflected in the results of the 1984 and 1985 experiments. Probably for the reasons given above.

In the 1984 experiment on trout, emigration rate was negligible until swim-up occurred (at c. 180% development to median hatch). At the lowest

velocity emigration rate was low (<0.12 day^{-1}) but was sustained at values above 0.02 day^{-1} from 180% development to 257% development to median hatch. In contrast, at the three higher velocities rates of up to 0.24 day^{-1} were observed but these were maintained for a shorter period (Figure 3). At the close of the experiment population density was similar in all four channels and rates of emigration were low. The main conclusions to be drawn from this are:

1. As might be expected, there was little emigration before swim-up (at 180% development to median hatch).
2. Soon after swim-up the rate of emigration increased and was maintained at a high level, possibly until an optimum population density was attained. In the 1984 experiment this density was in the range 8.6-16.6 fish m^{-2}.
3. Although emigration rate was shown to be related to water velocity (1983 experiments) there is no evidence that it is necessarily confined to a particular stage of development (Figure 3) or that final density bears a definable relationship to velocity treatment (Table 8). The results suggest that water velocity influences the rate of adjustment to an optimum population density but there is no indication that velocity necessarily influences the "target" density.

Interpretation of the 1985 results is a little more complex. The high emigration rates observed during the first two days after introduction of the salmon are best disregarded. They represent an exodus of fish which were at or very close to swim-up at the time of introduction to the channels. As flow in the channels only began the day before introduction, there would be negligible food material in the channels and speedy departure might be

expected. However, by the time the main body of salmon emerged from the gravel (at c. 170% development to median hatch) conditions within the channels would be more similar to those of a natural stream. Rates of emigration in the three highest velocities rose soon after swim-up to values of 0.1 to 0.2 day^{-1} and then fell to values of less than 0.05 day^{-1} by 15 June, to give population densities of 5-7 fish m^{-2} on 20 June. In contrast, at the lowest velocity, emigration rates rose to values 0.15 to 0.35 day^{-1} and these high values were maintained until 18 June, by which time there were few fish left in the channel (1.5 m^{-2} on 20 June). These results resemble those from the 1984 experiment on trout in indicating that appreciable emigration begins soon after swim-up. In the three higher velocities it is possible that population densities were adjusting towards a value of c. 6 m^{-2}. However, the sustained high emigration rate and the low final population density at the lowest velocity suggests that this velocity was actively avoided by the salmon, hence that the "target" density was influenced by the water velocity.

During the experiments on trout and salmon in 1984 and 1985 over 95% of the fish leaving the channels were found to do so during the part of the day which contained the hours of darkness. This confirms, for both species under constant velocity conditions, an earlier observation by Ottaway & Clarke (1981) for salmon. All of these observations were made under conditions of constant water velocity. The time of day of emigration under fluctuating flow conditions (e.g. 1983 experiments) is not known. Should emigration in this type of experiment also occur mainly at night then, as the velocity was changed in daylight, it implies that fish emigration rate

was influenced mainly by the velocity treatments rather than by the immediate effect of the change in velocity. This point is worthy of further examination.

The results presented above from the 1984 and 1985 experiments have been subject to preliminary analysis only. During 1985-6 more detailed analysis is proposed and up-dating of the results and conclusions may then be worthwhile.

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